ON THE MANUS AND PES OF *THYLACOLEO CARNIFEX* OWEN (MARSUPIALIA)

by R. T. WELLS* and B. NICHOL*

Summary

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An articulated left and right manus and a partially disarticulated left pes of the cave lion *Thylacoleo carnifex* were recovered recently from a Pleistocene cave deposit at Naracoorte, South Australia. The structure of the manus and pes is described. The manus is digitigrade with limited flexion in digits II, III, IV and V. Digit I is extremely robust, bears a large hooded ungual crest and is pseudopposable to a spatulate pisiform. The pes is plantigrade with major part of the weight transferred through the astragalus to the calcaneum. Analysis of the structure of the pes indicates syndactyly and the presence of a divergent hallux. The manus and pes show structural affinities with the arboreal phalangerids.

Introduction

Thylacoleo carnifex Owen (1859), the "flesh eating marsupial lion", was described from skull fragments from a late Pleistocene deposit at Lake Colangulac, Victoria. Although the tooth formula of such thylacoleonids is typically phalangeroid, the animals are characterised by development of exceedingly large sectorial upper and lower third premolars, large conical upper and lower first incisors and a marked reduction in the remaining incisors, canines and molars. The niche occupied by *T. carnifex* therefore has been the subject of considerable speculation (vide Gill 1954; Finch 1971). However recent studies of jaw mechanics (Finch 1971) tend to support Owen's conjecture that it was a large carnivore.

Finch (1971) made a preliminary analysis of the skeleton and suggested that the relatively long fore-limb may be used to strike at prey in a fashion similar to that of *Sarcophilus*. This suggestion relied partly upon her interpretation of the paw as a strong and heavy structure in which the digits could not be widely separated. However the structure of the pes was unknown to her, as the major portions of the hind feet are missing from all the skeletal material previously reported. The following is a preliminary description of the general morphology and arrangement of the bones of the manus and pes of this enigmatic animal.

Materials and methods

During excavations at Victoria Cave, Naracoorte, numerous skeletal elements of *Thylacoleo* were collected including the articulated right and left manus with portions of the fore-limb in association. The specimens were held together by a patina of calcite. In the laboratory the left manus was partially cleaned, but left in its fused state; the right manus was carefully disassembled, each element cleaned and then reassembled (Fig. 1). In the course of preparation of the right manus the cuneiform and pisiform of the left manus were recovered from the sediment.

All specimens removed from the Victoria Cave deposit are allotted numbers indicating their positions in a three-dimensional grid (Wells 1975). During the sorting of bone material, portions of a disarticulated left pes bearing similar grid reference numbers were recovered. This partial pes (Fig. 3) is not referable to any extant marsupial, nor could it be attributed to any extinct form for which the foot structure is known. The calcaneum is consistent with one recovered with skeletons from James Quarry, Naracoorte (M. Plane, pers. comm.). The close proximity of *Thylacoleo*

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P 16679

Fig. 1. Assembled right manus (P16679) of *T. carnifex*. The 5th medial phalange, cuneiform and pisiform are missing from this specimen.

tibia and fibula, and similarity in proportions to the manus, suggest that it is indeed the pes of *Thylacoleo*.

The following specimens and casts of the assembled right manus and left pes are lodged at the South Australian Museum:

P16678: left manus including fused carpus P16678a, cuneiform P16678b, pisiform P16678c, fused metacarpus P16678d, fused proximal and medial phalanges. P16678e, distal phalanges P16678f.

P16679: right manus including scapholunar P16679a, trapezium P16679b, trapezoides P16679c, magnum P16679d, unciform P16679e, metacarpals I to V P16679f, g, h, i, j respectively, proximal phalanges I to V P16679k, l, m, n, p respectively, medial phalanges II to IV P16679q, r, s respectively and distal phalanges I to V P16679u, v, w, x, y respectively and sesamoids P16679z.

P16680: left pes including astragalus P16680a, calcaneum P16680b, cuboid P16680c, navicular P16680d, metatarsals II, III, IV V P16680e, f, g, h respectively.

General description of the manus

The manus of *Thylacoleo* includes the carpus, metacarpus, phalanges and certain sesamoids associated with them (Figs 2A, B). The carpus is composed of seven bones arranged in two transverse rows. Articulating with the distal row of carpals are five metacarpals. Four of the five metacarpals are closely apposed, and each bears three phalanges. Metacarpals II–V show little lateral mobility, whereas the first (which is considerably shorter and more robust) bears only two stout phalanges. The distal phalange of the first digit bears an extremely large ungual crest and ungual process, suggesting the presence of a large recurved claw or unguis. Unlike digits II to V, the first is capable of considerable divergence as well as flexion. It appears to be opposable to a broad spatulate pisiform rather than to the remaining digits.

Carpus: In *Thylacoleo* there has been a loss and fusion of carpal elements to produce two rows which have a transverse convex cranial outline and a concave caudal one.

The proximal row is composed of three elements, the scapholunar (a fusion of scaphoid and the lunar) the cuneiform and a sesamoid, the pisiform. The scapholunar articulates with the distal end of the radius and bears on the trapezoides, trapezium and portion of the medial face of the magnum. The cuneiform, or ulnar carpal is greatly reduced. In comparison with most mammals it is a small, wedge-shaped bone concave on the proximal surface for receipt of the styloid process of the ulnar, and convex on the distal surface where it inserts in a basin in the unciform. It broadens caudally and bears a facet on the proximal surface at the point of attachment of the pisiform. The pisiform is short, broad and dorso-ventrally flattened and slightly expanded distally.

The distal rows of carpals is composed of: trapezium, trapezoides, magnum and unciform. The trapezium (carpale 1) is a small flattened bone in the form of a partial helix. It articulates laterally with the trapezoides and distally with the first metacarpal; the proximal end inserts in a notch in the palmar face of the scapholunar. Small rotations of the trapezium about its articulation with adjacent carpal bones result in considerable lateral-medial displacement of the first digit.

The trapezoides (carpale 2) is a small wedge shaped, proximo-distally compressed bone the

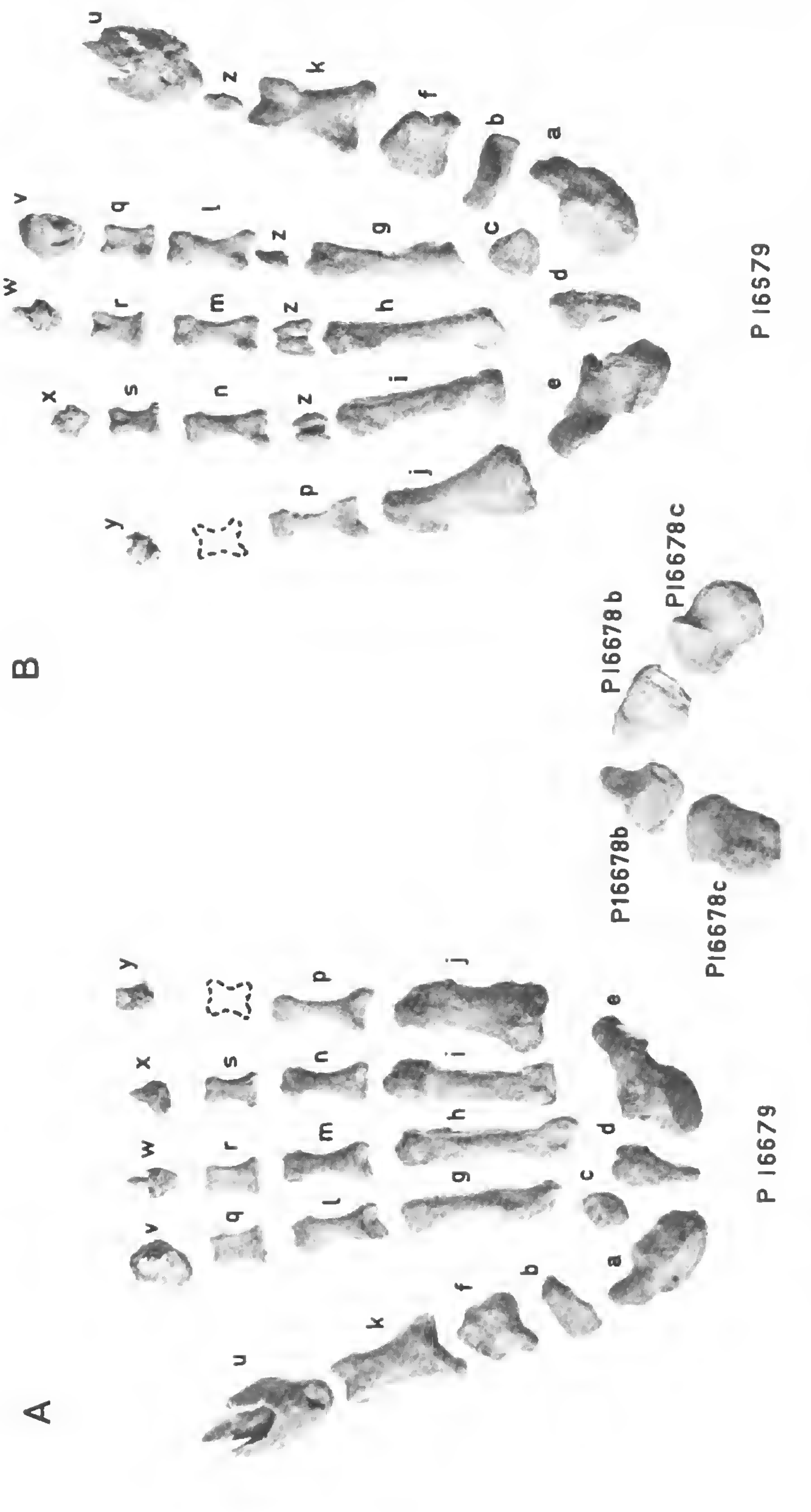

Fig. 2. Elements of the right manus and cuneiform and pisiform of the left manus of *T. carnifex* (A) dorsal view (B) palmar view. a, scapholunar; b, trapezium; c, trapezoides; d, magnum; e, unciform; f, g, h, i, j, metacarpals I-V resp.; k, l, m, n, p, proximal phalanges I-V resp.; q, r, s, t, medial phalanges I-IV resp.; u, v, w, x, y, distal phalanges I-V resp.; z, sesamoids.

P16680

Fig. 3. Dorsal view of the partial left pes (P16680) of *T. carnifex*. The cuneiforms, metatarsal I, portion of metatarsal IV and the phalanges are missing from this specimen.

ventral face of which is approximately triangular in outline. It articulates proximally with scapholunar, medially with the trapezium, distally with metacarpal II and laterally with the magnum. The magnum (carpale 3) forms a triangular wedge between the scapholunar and the unciform which bear on it medially and laterally respectively. It has a narrow medially-laterally flattened palmar projection. It bears distally mainly on the third metacarpal with a small portion bearing on the oblique lateral projection of metacarpal II.

The unciform (carpale 4) is the largest bone in the carpus, its lateral aspect is convex and extends down in a continuous curve behind the fifth metacarpal. A depression in the middle of the proximal face receives the distal portion of the cuneiform. The convex palmar face of this bone bears facets which articulate with metacarpals IV to V and the lateral face of the magnum.

Metacarpus: There are five metacarpals here numbered I to V from the medial to the lateral side. Metacarpal I is exceedingly robust, being almost twice the cross-sectional area of the remaining four metacarpals, yet only one-third as long. The expanded head of metacarpal I articulates proximally with the distal end of the trapezium and at its furthermost lateral displacement contacts the medial face of metacarpal II close to its proximal end.

Distally the axis of articulation of metacarpal I with the proximal phalanx is rotated medially approximately 30° to the axis of articulation with the trapezium. Metacarpals II, III, IV are closely apposed slender bones, medially-laterally flattened and rectangular in cross section. Metacarpal II is slightly shorter than III and IV which are of almost equal length. The proximal ends of these bones are expanded and displaced laterally; the shape of the articulating facets restricting movement to the dorso-ventral plane. Metacarpal II bears proximo-medially on the trapezoides and to a lesser degree proximo-laterally on the magnum. Metacarpal III bears proximo-laterally on the lateral face of the magnum while metacarpal IV inserts proximally in a notch in the unciform.

Metacarpal V differs from II, III and IV in the possession of a pronounced lateral flange, and lacks the expansion and lateral displacement of the proximal end; the articulating facet suggesting a small degree of lateral-medial rotation in addition to the dorso-ventral.

Phalanges: Digit I composed of a proximal and distal phalanx is extremely robust, the proximal portion being approximately 3X the cross-sectional area and 1.5X the length of the adjacent proximal phalanges. The distal phalanx bears a large ungual crest and ungual process. Digits II to V, although containing a medial as well as a proximal and distal segment, are overall slightly shorter than those of digit I. All the distal segments bear the sheathing base of small hooded claws. The ungual process of these segments is relatively long and slender and is less recurved than that of digit I.

Sesamoid bones: On the palmar surface of the metacarpophalangeal joint of digits III and IV are two sesamoid bones articulating primarily with the head of each metacarpal, and secondarily with the palmar tubercles of each proximal phalanx. A single sesamoid was found associated with the metacarpophalangeal joint of digit II; the small sesamoid found adhering to the proximo-distal phalangeal joint of digit I is probably the other element in this pair.

The mechanism of the grasp in the manus

The relationship between articulating facets was used to determine the range of movement between adjacent bones. A lateral view of the range of movements in digits II, III, IV and V is depicted in Fig. 4—in the extended position (A) and flexed (B). The distal phalanges are prevented from opposing the palm by restricted movement at the metacarpo-phalangeal joint and to a lesser extent at the proximo-medial phalangeal joint.

In dorsal view, with digits extended (Fig. 5), the extreme divergence of digit I and the slight divergence of digit V contrasts markedly with the close apposition of digits II, III and IV.

The range of latero-medial movement in digit I, and its relationship to the pisiform, is

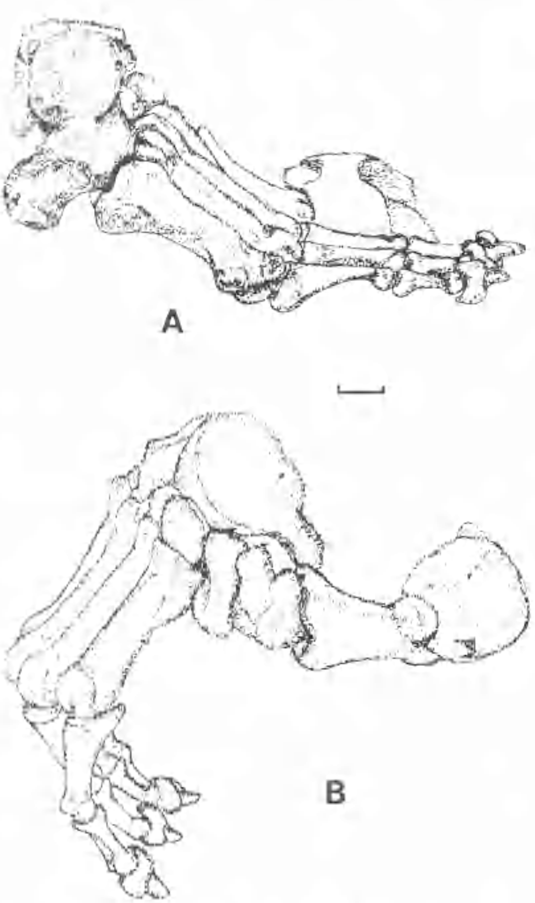

Fig. 4. (A) Lateral view of the right manus of *T. carnifex* with digits fully extended; (B) Medial view of the right manus of *T. carnifex* with digits fully flexed.

also shown in Fig. 5. Flexion of digit I and the pisiform would bring them into close opposition and it is suggested that this is the primary grasping movement. With the digits in their most divergent position it can be seen that the plane of the grasp is almost at 90° to the remaining digits. A similar grasp is found in the brushtailed possum *Trichosurus vulpecula* (Breeden & Breeden 1970).

Description of the pes

The skeleton of the pes in mammals is composed of the tarsus, metatarsus, phalanges and associated sesamoids. The following bones are missing from the partial pes recovered from the Victoria Cave: the cuneiform bones of the distal row of the tarsus, the first metatarsal, all the phalanges and any associated sesamoids, Fig. 6A, B.

Tarsus: The tarsus normally consists of seven tarsal bones arranged in two rows with a central bone, the navicular, between. The proximal row consists of the astragalus and calcaneum. In *Thylacoleo* the tibia and fibula articulate only with the astragalus which is the second largest bone in the tarsus. It articulates proximally with the tibia and fibula, distally with the navicular and ventrally with the calcaneum and the proximal dorsal surface of the cuboid. The proximal surface of the main body of the astragalus bears a shallow trochlea groove which articulates with the distal process of the tibia, an oblique lateral facet articulates with the lateral malleolus of the fibula. The astragalus articulates with the calcaneum by two distinct facets, a lateral concave one and a medial convex one. The distal portion, (head of the astragalus) bears a large convex, rounded facet which articulates with the navicular.

The calcaneum is the largest and longest bone of the tarsus. It bears two facets on the

Fig. 5. Dorsal view of the right manus of *T. carnifex* showing digits II to V fully extended with digit I flexed. The outline of the cuneiform and pisiform was produced from a mirror image of those from the right manus.
Inset—depicts dorsal view of digit I in extended position.

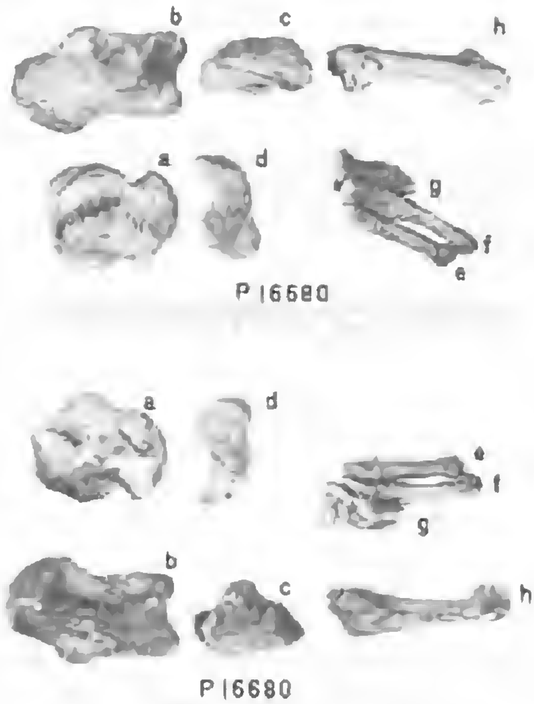

Fig. 6. Elements of the left pes of *T. carnifex* upper = dorsal view; lower = ventral view. a, astragalus; b, calcaneum; c, cuboid; d, navicular; e, f, g, h, metatarsals II, III, IV, V.

proximal surface which articulate with those on the distal surface of the astragalus to form a stable interlocking joint. The calcaneal tuberosity is short, robust and slightly flared caudally. The distal surface of the calcaneum is deeply grooved dorso-ventrally where it articulates with the proximal surface of the cuboid. The navicular is the central bone in the tarsus, it articulates proximally by way of a large concave latero-medial facet with the astragalus, ventrally by way of a small concave facet with the cuboid and distally by way of a large latero-medial convex facet with the missing cuneiforms. A pronounced tuberosity on the distal medial surface may articulate with the proximal portion of the missing medial cuneiform. The remaining tarsal bone, the cuboid, appears to be as long as the combined length of the navicular and the missing cuneiforms. It articulates proximally by way of a long narrow facet with the dorso-ventral groove in the distal face of the calcaneum. Two small facets occur on the dorsal surface; the larger proximal one articulates with the astragalus while the smaller anterior one presumably articulates with the missing lateral cuneiform. It bears a small plantar process. The distal end forms a large slightly recurved oval surface which for 4/5th of its length articulates with the proximal surface of metatarsal V and for 1/5th with the lateral portion of the proximal surface of metatarsal IV.

Metatarsus: Metatarsals II, III and the proximal portion of IV were found fused together and in the vicinity of metatarsal V. A latero-medial section through the assembled metatarsals has a convex dorsal outline and concave ventral one (Fig. 7).

The structure of metatarsal I is unknown, but the presence of a medial distal tuberosity on the navicular is suggestive of a divergent hallux comparable to *Trichosurus*. Metatarsals II and III are relatively short and slender bones, their close apposition and general form is similar to that of the syndactylous toes in *Trichosurus*. The size of the proximal portion remaining of metatarsal IV and its relationship to metatarsals III and V indicate that it may have been the longest of the three. The lateral half of the proximal facet on metatarsal IV articulates with the dorsal 1/5th of the distal facet of the cuboid. A small proximo-lateral facet articulates with the proximo-medial face of metatarsal V. Metatarsal V is the most robust of all four. It bears pronounced tuberosities on the proximal and distal latero-ventral surfaces. A large proximal facet articulates with the cuboid, while a small ventro-medial facet articulates with metatarsal IV.

In *Thylacoleo* the greater part of the body weight supported by the hind limbs is transferred from the astragalus onto the calcaneum and portion of the cuboid. The surface area of articulation of the calcaneum with the distal tarsals is 20% larger than that of the astragalus suggesting a distribution of weight through these elements to the metatarsals in the ratio 3:2. The larger portion of the weight is borne

Fig. 7. Distal view of proximal surface of metatarsals 2, 3, 4 and 5.

by metatarsal V and a small portion of IV, while the remaining 40% is borne by digits I, II, III and a portion of IV. However the slender nature of metatarsals II and III, and the presence of a pronounced medial tuberosity on the navicular, suggests that much of this load is borne by a robust divergent hallux.

The shallow trochlea groove, the plantigrade nature of the stance (Fig. 3), the apparent syndactyly of digits II and III and the inferred presence of a large divergent pollex are characteristics which in Australian marsupials resemble most closely the pes of phalangerids.

Discussion

The digits of the hands of most mammals diverge when extended, and converge when flexed (Haines 1958). Such hands are considered suitable for scrambling over rough ground and, if clawed, to climbing; however they appear unsuitable for gripping branches of trees unless used in a clasping manner as is the case with *Didelphis virginiana* (Haines 1958). Cartmill (1974) examined the non-primate arboreal sciurids, and concluded that in the structure of the hand the arboreal genera were distinguishable from the terrestrial forms only by their longer 4th digits and carpal pads and sharper, more recurved claws. Bishop (1964) found little anatomical difference in the hands of terrestrial and arboreal carnivores.

Animals which climb by grasping branches e.g many primate species, usually have prehensile hands. If carpo-metacarpal movement is restricted to one plane, the divergent thumb is classified by Napier (1961) as pseudo-opposable but opposable if the thumb can rotate about the carpo-metacarpal joint so as to oppose the remaining digits.

In primates the degree of curvature of the carpal arch is related to the extent of opposability of the thumb and to the size and functional nature of the long flexors of the digits. These lie in a tunnel formed by the carpal arch and the flexor retinaculum which binds the two sides of the arch together (Napier 1961). A deeply curved carpal arch is characteristic of animals in which flexing of the digits plays a major role in locomotion and is likely to be similarly deepened and strengthened to match the exerted stresses of clasping during climbing.

The manus of *Thylacoleo* exhibits several paradoxical features. (a) Digit I is capable of wide divergence, and is pseudo-opposable yet digits II, III and IV show little divergence or convergence; (b) Digit V could diverge slightly; (c) All digits are clawed, the ungual crest on digit I being extremely robust and recurved while those on the remaining digits are small and slender with little recurvature; (d) the carpal arch is deep and robust yet the digits with the exception of I, are capable of only limited palmar flexion.

TABLE 1

Habit and digital formula of the manus of some marsupials

Habit	Species	Digital formula of manus
Arboreal	*Phascolarctos cinereus*	4>3>2>5>1
Arboreal	*Pseudocheirus peregrinus*	
Arboreal	*Acrobates pygmaeus*	
Arboreal	*Cercartetus concinnus*	
Arboreal	*Petaurus breviceps*	4>5>3>2>1
?	*Thylacoleo carnifex*	3>4>2>5>1
Arboreal	*Trichosurus vulpecula*	
Arboreal/Terrestrial	*Dasycercus cristicauda*	
Arboreal/Terrestrial	*Dasyurus viverrinus*	
Arboreal/Terrestrial	*Antechinus flavipes*	
Arboreal/Terrestrial	*Sminthopsis crassicaudata*	
Terrestrial	*Vombatus ursinus*	
Terrestrial	*Macropus eugenii*	
Terrestrial	*M. giganteus*	
Terrestrial	*Thylacinus cynocephalus*	
Terrestrial	*Sarcophilus harrisii*	
Terrestrial	*Isoodon obesulus*	3>2>4>5>1
Terrestrial	*Macrotis lagotis*	

Finch (1971) suggests that compared with other marsupials *Thylacoleo* has relatively long limbs, and that the almost equal length of fore and hind limbs implies a cursorial mode of locomotion. However she also notes that the scansorial (*Trichosurus*) and koala (*Phascolarctos*) have "fairly long fore limbs" but have, in contrast to *Thylacoleo*, mobile digits on the forepaws which enables the animal to maintain a firm grasp of the branch of a tree. From our analysis of the manus of *Thylacoleo* we conclude that, in spite of the limited convergence in digits II, III and IV the animal does indeed have an efficient and powerful grasping mechanism in the opposition of digit I to the pisiform. Furthermore although the manus would adopt a digitigrade stance on a horizontal surface it would be ideally adapted to a climbing grasp. Tree frogs of the family Hylidae illustrate this point very well. However as pointed out by Bishop (1964) there is little anatomical difference in the hands of terrestrial and arboreal carnivores, a hand well adapted to a climbing grasp could equally well be adapted to holding prey or both. The structure of the hind foot of *Thylacoleo* suggests a plantigrade stance when on a horizontal surface. Due to the absence of the cuneiforms and digit I of the pes, speculations about its functions are less meaningful, nonetheless it is remarkably similar in form and structure to the pes of the brushtailed possum (*Trichosurus*) which is used mainly in a clasping manner. The slender nature of metatarsals II and III and their close apposition is strongly indicative of syndactyly and is consistent with its proposed phalangeroid ancestry.

Table I lists the digital formulae of a range of marsupials. The truly arboreal forms among the phalangeridae all have the typically long 4th digit similar to Cartmill's (1974) arboreal sciurids. The digital formula for the manus of *Thylacoleo* is similar to a large range of semi-arboreal marsupicarnivores and terrestrial herbivores.

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SALT CRUST SOLUTION DURING FILLINGS OF LAKE EYRE

BY J. A. DULHUNTY

Summary

Investigations of solution of salt crust during the minor (1973) and major (1974) fillings of Lake Eyre were carried out in relation to water depth, salinity layering and wave action. When water depth exceeded half the maximum wavelength of surface waves, a saturated brine layer formed over residual salt crusts and retarded solution. Following the filling in February 1974, a large area of the thickest crust in central Madigan Gulf survived to the end of 1975 or early 1976, when water level fell to less than half maximum wavelength, and the residual crust dissolved; the thickest part of the Belt Bay crust survived until after September 1974 but dissolved by August 1975; in Jackboot Bay the thickest crust dissolved by September 1974.

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Introduction

Salt crusts, up to 46 cm thick, rest on Quaternary sediments in the southern bays of Lake Eyre North (Bonython 1956; Dulhunty 1974). Small inflows of river water covering parts of the lake bed, termed minor fillings, frequently dissolve some of the salt, but it is soon redeposited by rapid evaporation. On widely spaced occasions, as in 1949 and 1974, sufficient water enters the lake to cover the whole of its bed and dissolve all the salt crusts. On such occasions, referred to as major fillings, it has been assumed that the salt crusts rapidly dissolve; newly introduced sediments are deposited, and then new salt crusts reform on top of the sediments as brines evaporate. However, no precise or quantitative investigations have previously been made on the solution of salt during fillings of the lake, although redeposition of salt after the 1949 filling was described by Bonython & Mason (1953), and Bonython (1956).

The distribution and thickness of salt crusts in the southern bays of Lake Eyre North, were surveyed under dry lake conditions in 1972 (Dulhunty 1974). In 1973 a minor filling of the lake occurred when a limited quantity of water entered from the Warburton River during May, June and July. It flowed to the south-western corner of the lake filling Jackboot and Belt Bays, where solution of salt was examined in July 1973. By late December 1973 the whole of the water had evaporated and the dissolved salt was redeposited, and the lake had returned to a dry condition, as reported by Mr M. O. Hughes of Muloorina Station.

Early in 1974 Lake Eyre filled to the greatest known depth since European settlement, and possibly for 500 years (Dulhunty 1975). The lake commenced to fill early in February 1974 and remained full throughout 1975 and 1976 during which time the solution of salt was investigated in relation to water depth, salinity layering and wave action; results are recorded in this paper.

Methods of investigation

Areas of undissolved salt crust were found by probing the lake bottom with a long pole from a boat. Where salt crust was present the pole hit its surface with a resounding impact and tended to bounce. Where it was absent, the pole penetrated the soft silt which had underlain the crust before it dissolved. This provided a simple, reliable and positive test for presence or absence of salt crust beneath lake waters. Areas of residual crust were mapped by running pole tests at intervals along predetermined lines, and plotting results.

The thickness of a residual salt crust was measured by boring from a boat anchored by three radially disposed concrete blocks.

A 15 mm wood-boring auger was attached to lengths of 12.5 mm water pipe, screwed

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together so as to extend about 1 m above the surface of the water when the auger rested on the salt crust. A wood-boring brace was attached to the upper end of the piping. A long pole was then lowered vertically to rest on the salt beside the auger, and the position of a mark near the top of the boring pipe was noted on a scale attached to the pole. The auger was then rotated by means of the brace, and the depth penetrated into the salt by each rotation was measured on the pole scale as the pipe moved down. When the auger reached the base of the salt crust and broke through into the soft underlying silt, the depth of penetration measured gave the thickness of the crust.

Water samples for salinity determinations were collected at different depths by lowering the weighted end of 12.5 mm hose to the required level and then slowly pumping water up through the hose to remove that taken in during the lowering. Further water from the required level was then pumped slowly into a sample bottle. Densities of the water samples were measured very accurately, and their salinities, in terms of grams of Lake Eyre salts per litre of solution, were determined from density-salinity relations previously established by solution of known weights of Lake Eyre salts in water, and by gravimetric measurement of total dissolved solids per litre of Lake Eyre brines.

Results

Major Filling, 1974

The dry lake bed survey of salt crust thickness and distribution (Dulhunty 1974) was carried out about 18 months before the major filling commenced in February 1974. This provided an excellent basis of pre-filling control data for investigation of the progressive solution of salt crusts which occupied almost two years.

The principal investigations were carried out in Madigan Gulf where the largest and thickest salt crust occurred before the filling. Dulhunty (1974) termed the place of thickest salt and lowest height value 'Centre Point' and noted it to be about 10 km southerly from the point of thickest salt and lowest height recorded by Bonython (1956).

At various stages throughout the investigation, salinities were determined for water from the surface and at different depths, as shown in Figs 1B and 1C. The 12 values shown along the salinity curve in Fig. 1B are measured values. Five were obtained from water samples collected in Level Post Bay (2 in March 1974, 1 in December 1974 and 2 in March and April 1975), and the other 7 were from samples collected at Centre Point. The steep salinity gradient in bottom waters overlying residual salt crust, illustrated in Fig. 1C, was obtained by measurement of salinities in samples collected from bottom waters at Centre Point and along line A–B in Fig. 1A, during July 1974. Residual salt crust thicknesses shown along the salt crust thickness curve in Fig. 1B, were measured by borings at Centre Point, at stages during progressive solution of the crust.

The curve for water depth in Fig. 1B represents the mean of a large number of gauge board readings in Level Post Bay and soundings at Centre Point. The depth values shown along the curve are mean values at different places to facilitate reading of the diagram. The fall of about 0.4 m between November 1975 and March 1976, is based on interpolation between readings in October 1975 and April 1976. Unfortunately no readings were made between these dates, but the level must have fallen, as a result of evaporation, by at least as much as it did during the same period in 1974–75 (see Fig. 1B). No water entered the lake during either of these summer periods. Also observations of shoreline wave cut features, beneath water level later in 1976, indicated that the lake had fallen to a level equivalent to a depth of about 3.2 m at Centre Point. Therefore a fall to this depth is believed to have occurred early in February 1976. An appreciable volume of water entered the lake from the Macumba and Neales Rivers and Frome Creek late in February 1976, raising lake water towards the levels measured in April, May and June of that year.

The margin of the original salt crust before the 1974 filling, is shown in Fig. 1A extending almost to the shorelines of Madigan Gulf. To the northwest the salt crust thinned out and disappeared where the Gulf opened on to the Slush Zone of very thin discontinuous salt overlying soft mud and slush extending across the full width of the lake (Dulhunty 1974).

It had been generally assumed that the salt crusts of Lake Eyre rapidly passed into solution as soon as a volume of water in excess of that which would have been sufficient to dissolve all the salt, entered the lake. The 1974 filling of Lake Eyre North commenced in February, and after six months filling with a volume of water far in excess of that neces-

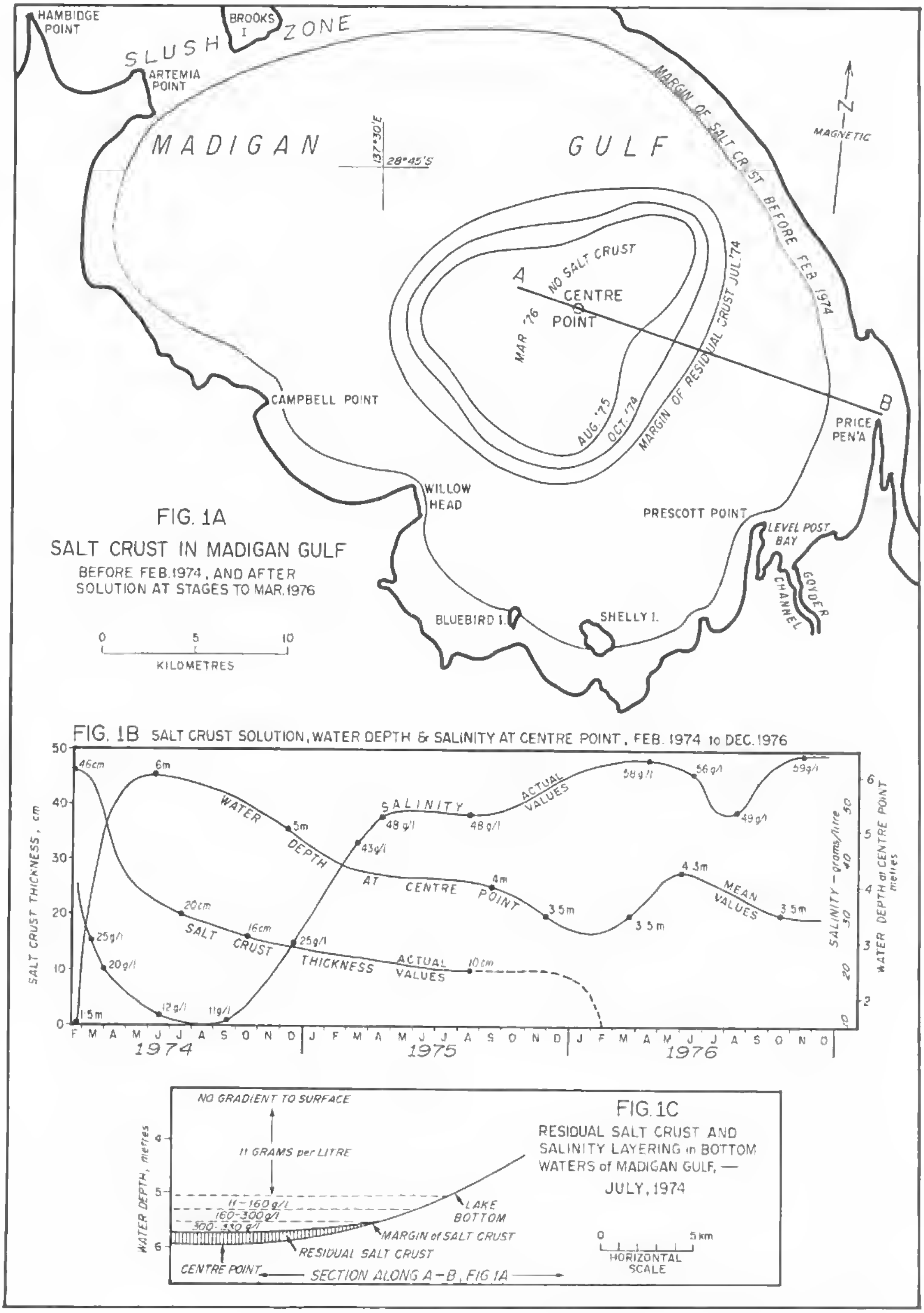

Fig. 1. Relations of salt solutions to water depth and salinity in Madigan Gulf.

sary to dissolve all the salt, a residual area of crust remained undissolved in the central area of Madigan Gulf. Its margin, determined by pole test survey in July 1974, was as shown in Fig. 1A. Further surveys in October 1974 and August 1975 showed progressive, but slowing solution of the residual crust to the positions shown in Fig. 1A. Pole tests by R. Clarke and M. Atkinson in August 1976 and by the author in November 1976, established that the whole of the residual crust had gone into solution.

Measurements of salinity at different depths, in July 1974, established a saturated brine layer from 10 to 20 cm deep on the solution surface of the salt crust. Above the brine layer, there existed relatively high salinity water up to 50 cm deep with a high salinity gradient. The saturated brine layer did not extend more than 1 km, and the overlying high salinity water more than 5 km beyond the edge of the salt (Fig. 1C). Away from the area of residual salt crust, where salt had been completely dissolved, the lake waters exhibited very little, if any, salinity gradient, and no saturated brine or high salinity water existed on the bottom.

The bottom saturated brine layers were always almost opaque black in colour, rich in dissolved hydrogen sulphide, and carried finely divided organic debris and clay which appeared to be almost colloidal, but could be separated by filtration.

Minor Filling, 1973

The minor filling of Lake Eyre during May, June and July 1973 covered Belt and Jackboot Bays and an area west of Hunt Peninsula to a level of −13.6 m A.H.D. It gave maximum water depths of 1.58 m to the base of salt crusts in Belt Bay and 1.43 m in Jackboot Bay. Some water, when aided by westerly winds, flowed east round Hambidge Point into Madigan Gulf covering parts of its bed to depths of less than 0.5 m.

During July 1973, pole test surveys for salt in Jackboot and Belt Bays indicated the presence of relatively large areas of residual salt crusts beneath the water cover, where the thickest crusts were found in 1972 (Dulhunty 1974) and the deepest water occurred in 1973. Thicknesses of residual crusts were measured by boring and water samples were collected for salinity determinations. Approximately one third of the original thickness of crusts had been dissolved by late July 1973, under the conditions which existed during the filling, producing salinities of 186 and 235 *g/l* in Belt and Jackboot Bays, respectively. The small amount of water which reached Madigan Gulf covered part of the salt crust in central areas of the Gulf and extended almost to Willow Head. Measurements 3 km northeast of Willow Head showed that about 12 mm of crust had been dissolved by the end of July when water salinity reached saturation at about 325 *g/l*.

Salt solution in Jackboot and Belt Bays, 1974–75

Only limited opportunity was available for investigation of salt crust solution in Jackboot and Belt Bays during the 1974 filling. Surveys of these bays were made early in September 1974, to ascertain the extent to which salt solution had occurred. Pole test traverses in Belt Bay indicated a roughly circular residual area of salt crust, about 2.5 km in diameter, where the thickest salt occurred in 1972, immediately to the northwest of a silcrete island situated 1.5 km west of Bonython Head. At a point 0.4 km west of the southern tip of the island, water depth was 5.8 m, salt thickness was 6 cm where it had been originally 29 cm, upper water salinity was 9.4 *g/l* and a gradient from 11 to 325 *g/l* occurred in 1 m of bottom water lying on the salt crust. This indicated a layer of saturated brine on the solution surface of the salt crust as in Madigan Gulf, and the 23 cm of salt dissolved was slightly less, but comparable with the 29 cm dissolved in Madigan Gulf by early September 1974. A pole test for salt immediately west of the silcrete island in Belt Bay, by R. Clark, and A. & M. Atkinson in August 1975, indicated that the Crust had completely dissolved, and a surface water sample collected at the same time gave a salinity of 29.2 *g/l*.

In Jackboot Bay it was found that the main salt crust had dissolved by early September 1974, with only occasional small patches of salt remaining on the bottom. Maximum water depth was 5.75 m and salinity of upper water was 11.8 *g/l* with a gradient from 13.4 to 15.0 *g/l* in 1.0 m of bottom water, where the salt crust had originally been 23 cm thick. This means that solution of 23 cm of salt had occurred in Jackboot Bay, as in Belt Bay, and that it had just removed all the main crust. No bottom brine layer was found in September 1974, due possibly to the small area of thick crust in Jackboot Bay, or dispersion after solution of the salt.

Conclusions

Salt crust solution in Madigan Gulf, 1974–76

It was evident that the saturated brine layer and overlying high salinity water regulated rate of solution of the crust. Where water depth was appreciably less than half the wavelength of wind waves on the surface, disturbance from wave action would have been sufficient to prevent the formation of a brine layer, and salt crust would have dissolved. At depths considerably in excess of half the wavelength, disturbance of bottom water would have been negligible and a brine layer could have formed over the salt. During the strongest winds experienced on the lake, wavelengths of 8 m were measured suggesting that salt crusts at depths of less than 4 m would dissolve relatively quickly, but at greater depths they could be protected by overlying brine layers. Therefore the history of salt crust solution in Madigan Gulf during the 1974 filling, appears evident from relations between salinity, water depth and rate of solution of salt illustrated in Fig. 1B.

With early vigorous inflow of relatively shallow water across the lake bed during February and March 1974, solution of salt was very active. Crust thickness was quickly reduced from its original thickness of 46 cm at Centre Point, to about 28 cm, producing water salinities in excess of 30 g/*l*. Water depth increased rapidly until the end of May, reaching its maximum of 6 m in early June 1974. Depths in excess of half the maximum wavelength of wind waves were soon established. With lack of wave disturbance in bottom waters, brine layers commenced to form on the residual salt crust, slowing down rate of solution. This, and dilution of upper waters by enormous volumes of fresh water, reduced salinity of the upper waters to as low as 10 g/*l* in August. From September 1974 to October 1975, water depth and salinity increased, and the rate of salt solution slowed down and almost ceased by September 1975. Water level continued to fall reaching a depth of less than half the maximum wavelength during October where it remained until April 1976. In August 1976 no salt crust remained, and it is believed that it finally dissolved during the period from October 1975 to March 1976, as illustrated in Fig. 1C.

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